Distribution of Epifaunal Biomass on a Sublittoral Rock-Reef

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Previously the author reported on the quantitative distribution of epifaunal species and individuals and their zonation on a siltstone reef located in the open ocean near Corona del Mar, California (Pequegnat, 1964). A marked top-to-bottom reduction in numbers of species and individuals was observed to exist on this reef, and these changes were related to a reduction of wave-induced water movements from the reef's upper to lower levels. Three observations pointed to the desirability of determining the distribution of biomass over the rock-reef: (1) the populations of some species were greatest on the reef's lower levels, (2) several of the largest species with relatively small numbers of individuals occurred here, and (3) there appeared to be a shift from a preponderance of suspension-feeders at the top toward increasing importance of deposit-feeders and scavengers at the base.

Accordingly, the objectives of the present study were: (1) to determine the quantitative distribution of biomass over the reef's surface, and (2) to relate the observed pattern to (a) position on the reef, (b) feeding types, (c) the frequency of occurrence of species on quadrats, and (d) the number of individuals per species.

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STUDY SITE AND METHODS

Because descriptions of the study site and sampling methods used have been published elsewhere (Pequegnat, 1964), only a brief outline of them is given here. The rock-reef is located about 500 m offshore (referred to hereinafter as Reef 500) where, at mean sea level, its depth ranges from 9.5 m at the top to 18.5 m on the seaward bottom. Because the epifauna exhibits marked changes in composition down the reef, it has been subdivided into four zones. These zones, together with their general depth limits along the transect where the present sampling was done, are: Reef-top Zone, 9.5–12.5 m, where the important epifaunal feature is an incrustation formed by the rock oyster *Chama pellucida;* the Mid-reef Zone, 12.5–14.5 m, which supports a thick growth of calcareous ectoprocts; the Reef-base Zone, 14.5–16.5 m, where large sea urchins and deposit-feeding sea cucumbers predominate; and the Mixed-bottom Zone, 16.5+ m, which is located on the adjacent sea bottom of sediments and rock slabs and which supports a mixture of infaunal and epifaunal species. In the following sections the term reef-proper will embrace the first three zones, while the term reef-complex will include the mixed-bottom as well.

All samples were taken under water through use of conventional Scuba techniques. Small species were sampled on the reef-proper from 0.1 m^2 quadrats, and from 0.25 m^2 quadrats on the mixed-bottom. Quadrats encompassing 1 m^2 were used to sample large species (gorgonians, sea urchins, and the like) on the reef-complex. The animals taken in samples were sorted into species, counted, and weighed dry. These general procedures were followed prior to drying: (1) mollusks were removed from their shells, (2) all tubiculous species were processed without tubes, (3) echinoderms, large decapods, and the like were decalcified, and (4) sponge and ascidian mats were picked free of motile species and rinsed free of sediments in filtered sea water.

Samples were taken during parts of 1958, 1959, and 1963. Unless specifically stated otherwise, all tabular data are based upon samples taken during all three years.

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GENERAL DISTRIBUTION OF BIOMASS

The epifaunal biomass is clearly concentrated on the upper levels of Reef 500. From the totals shown in Table 1, it is apparent that the mean biomass of the Reef-top Zone is about twice that of the Mid-reef Zone, seven times that of the Reef-base Zone, and 15 times that of the Mixed-bottom Zone. Analysis of variance of the differences in biomass among the zones of the reef-complex are highly significant at the 99% level (Tabular F (.01) = 5.70). Even though the biomass of the mixed-bottom region is a small fraction of that of the reef-top, it is large compared with that of many level-bottom communities. This is attributed to the quantities of debris and detritus swept from the reef by the strong water movements.

The top-to-bottom decline in biomass is consonant with the general decline of species and individuals, but these two entities need not be causally related. The fact that they are so related indicates that environmental conditions exist at the top of the reef and not at the base that favor the development of species whose biological characteristics include production of large standing crops. All of the largest producers of biomass attain maximum population densities on the reef's upper levels, and most of them are sessile or sedentary suspension-feeders. Among these, in descending order of biomass per m^2, are the sessile pelecypod *Chama pellucida,* a sponge mat composed of such amorphous sponges as *Lissodendoryx noxiosa,* the sedentary, plankton-feeding sea cucumber *Cucumaria lubrica,* and the burrowing date mussel *Lithophaga plumula.* The conditions that favor maximum development of their populations, such as ample supplies of suspended material and suitable water movements, are present only on the reef's upper levels.

BIOMASS AND FEEDING TYPES

On a weight basis, suspension-feeders predominate in all zones of the reef-complex (Table 1). They are followed in order by carnivores, scavengers, herbivores, and deposit-feeders. The principal carnivores are, in descending order of standing crop, the starfish *Pisaster giganteus,* various nemerteans, eunicid polychaetes, and gastropod mollusks. Among the principal scavengers are such crabs as *Paraxanthias taylori* and *Lophopanopeus leucomanus,* the ophiuroid *Ophioderma panamensis,* and the hermit crab *Paguristhes ulreyi.* The chief herbivores are the algaphagous sea urchins, the limpet *Megathura crenulata,* and such chitons as *Callistochiton crassicostatus.* The deposit-feeders are represented by the sea cucumbers *Parastichopus parvimensis* and *Leptosynapta albicans,* and the terebellid polychaete *Amphitrite robusta.*

Table 1 reveals that on the reef-proper the mean weight of suspension-feeders decreases sharply from reef-top to base, as do the weights of carnivores and scavengers, though their decline is more gradual. Herbivores and deposit-

TABLE 1

DISTRIBUTION OF DRY-WEIGHT BIOMASS ON REEF 500 BY ZONES AND BY PRINCIPAL FEEDING TYPES*

FEEDING TYPES	REEF-TOP		MID-REEF		REEF-BASE		MIXED-BOTTOM		MEAN WT.
	g/m^2	% wt.	g/m^2	% wt.	g/m^2	% wt.	g/m^2	% wt.	
Suspension-feeders	2238.4	86.4	1120.4	79.6	202.5	53.9	55.6	31.9	904.2
Carnivores	219.8	8.5	128.0	9.1	53.9	14.3	25.0	14.3	106.7
Scavengers	122.8	4.8	117.1	8.3	45.1	12.0	63.3	36.3	87.1
Herbivores	4.1	0.2	37.6	2.7	63.3	16.9	6.6	3.8	27.9
Deposit-feeders	0.1	0.1	4.5	0.3	10.9	2.9	24.0	13.7	9.9
Totals	2585.2		1407.6		375.7		174.5		

* The marked drop in total biomass between the mid-reef and reef-base zones is accounted for in part by lack of water movement and by feeding activities of sea urchins that destroy settling larvae.

feeders, on the other hand, exhibit a marked increase of biomass toward the bottom.

These patterns of biomass distribution on the reef and among the feeding types coincide well with expectations for those on a sublittoral rock-reef so situated as to have significantly higher values of water movement and suspended matter at the top than at the base (resulting from surface-wave propagation). I have already demonstrated that such a pattern of water movement exists on Reef 500 (Pequegnat, 1964). Suspension-feeders are favored by active water movement, whereas scavengers and deposit-feeders are benefited by calm waters at the reef-base that permit deposition of debris and detritus. Nevertheless, it is apparent that all feeding types are represented at every level on the reef. This permits the development of true communities that make effective use of the products of the primary producers. Some insight into the efficiency of this utilization of organic matter is revealed by the fact that the standing crop of deposit-feeders on the reef is little more than 1% that of the suspension-feeders.

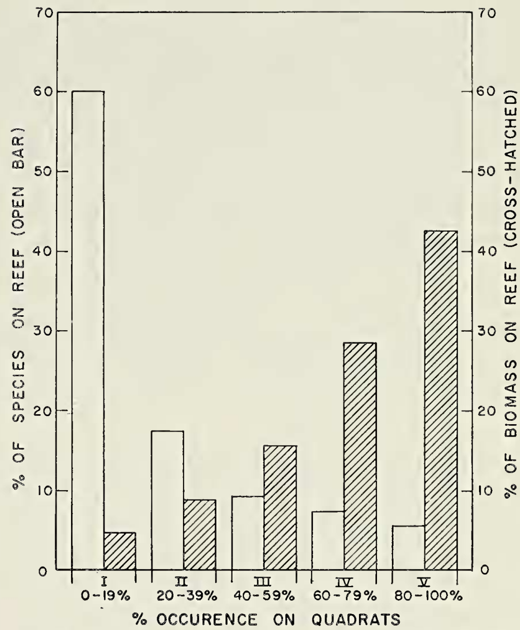

FIG. 1. The inverse relationship between per cent of species total and per cent frequency of species among quadrats, and the concentration of biomass in high-frequency species. Examples of species in the frequency groups I to V are given in the text.

FREQUENCY OF OCCURRENCE ON QUADRATS AND INDIVIDUALS PER SPECIES

The sublittoral epifauna displays a high degree of heterogeneity, i.e., a large percentage of species occur on a small per cent of quadrats, reflecting a poor fit of the Poisson distribution. This has a certain relationship to the production of biomass (Fig. 1). Of the 265 species of macroinvertebrates detected on the reef-proper, only 15 (6%) were found on 80–100% of quadrats (Group V), whereas 159 (60%) were found on only 0–19% of quadrats. But the latter group, even though 10 times as numerous as Group V, contribute only a tenth as much to the total biomass as do the 15 high-frequency species. Thus, the majority of species contribute very little to the standing crop biomass. Typical examples of each frequency group are: (I) the small gastropod *Seila montereyensis,* (II) the terebellid polychaete *Thelepus crispus,* (III) the holothuroid *Cucumaria lubrica,* (IV) the starfish *Pisaster giganteus,* and (V) *Chama pellucida.* The largest contributors to the biomass are suspension-feeders that are of intermediate size, have a tendency to aggregate, are broadly adapted to the changing physicochemical factors on the reef's vertical axis, and are either colonial or represented by large numbers of individuals.

Taking the species of the four most important noncolonial phyla on the reef-proper (viz., Mollusca, Arthropoda, Echinodermata, and Annelida), the mean number of individuals per square meter of those species occurring on 80–100% of quadrats is 283, while for the 0–19% group the mean drops to only 3. Apparently the multiplicity of microhabitats present on a rock-reef such as this favor highly adapted species whose small populations reflect the small area of each such habitat.

These findings may appear to support Turpaeva's (1957) conclusion that the basic nature of marine benthic biocoenoses can be ascertained from the dominant species alone. Perhaps this conclusion is valid for level bottom communities, but lack of critical information precludes its immediate application to complex epifaunal assemblages. We need to know that species selected as dominants on a standing crop basis retain this rank when secondary productivities can be calculated. Also, we need to be able to recognize successional stages in the sublittoral, for until we do it is impossible to assume that a small contributor to the biomass at one time interval is not an essential part of the community over a longer time-span.

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